SHELL SELECTION AND AGGRESSIVE BEHAVIOR IN TWO SYMPATRIC SPECIES OF HERMIT CRABS

WILLIAM C. GRANT, JR., AND KEVIN M. ULMER [1]

Williams College, Williamstown, Massachusetts, and Mt. Desert Island Biological Laboratory

There is abundant evidence that hermit crabs do not enter gastropod shells at random but select shells according to species type and associated characteristics of shape, shell covering, dimension and weight. Reese (1962a, 1963) and Orians and King (1964) concluded from investigation of shell selection behavior in several species of hermit crabs that both preference for and availability of different mollusc shells influence the frequency distribution of shell types occupied. Shell configuration, aperture size, shell weight/crab weight indices and shell weight/shell volume indices, *etc.* (Markham, 1968; Hazlett, 1970b) all provide important evaluation stimuli for selection. Shell entering behavior is elicited through tactile and proprioceptive stimuli from mechanoreceptors on chelipeds and periopods which trigger a sequential series of fixed motor patterns. Reese (1963) and Hazlett (1971) present evidence that such patterns develop in glaucothoe larvae at the time of their initial entrance into shells. Kinosita and Okajima (1968) have described a series of behaviors in the land hermit crab, *Coenobita rugosus,* in which "measurements" of shell aperture by probing and extension of chelipeds provide crabs with information for selection of larger shells as they grow.

In aggressive encounters which may be associated with competition for suitable shells and which may result in establishing dominant-subordinate relationships, hermit crabs display characteristic patterns of behavior. These have been analyzed in detail by Hazlett (1966a, 1967, 1968a, 1968b, 1970c, 1972a) and by Hazlett and Bossert (1965, 1966). Elevation of the body and extension of chelipeds provide effective signals for altering behavior in combatants. Increase in weight and visual shell size enhances the probability of a crab initiating or dominating an encounter although when size differences are pronounced larger animals tend to ignore display by smaller individuals. Shell size has no effect on the level of aggressiveness in *Pagurus hirsutiusculus* according to Vance (1973b) although Hazlett (1970b, 1970c) found that occupancy of inappropriately sized shells increased aggression in both *P. bernhardus* and *Clibanarius vittatus* individuals. Aggressive contact may be inter- or intra-specific depending on the species involved. According to Reese (1962b, 1964) attacks may be prevented if subordinate crabs assume submissive postures. The probability of a crab winning an encounter is influenced by its past history of success or failure as shown by Hazlett (1966b) and Mainardi and Rossi, (1971). According to Rossi (1971) dominant crabs are larger, obtain more food and molt more frequently. The investigations of Courchesne and Barlow (1971) and Hazlett (1966b, 1968c) have shown that isolation increases and aggregation decreases aggression, although agonistic be-

[1] Present address: Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

havior may increase with initial crowding until crabs have adjusted to new density levels.

In the sub-littoral zone of Frenchman Bay along the northeast shore of Mt. Desert Island, Maine two species of hermit crab *Pagurus acadianus* and *Pagurus pubescens* occur sympatrically. A ten-year survey (Grant, 1963 and more recent unpublished data) has shown that since 1967 *P. pubescens* has infiltrated areas just below low-tide level previously occupied exclusively by *P. acadianus*. The present studies were undertaken to investigate what role if any shell selection, shell availability and agonistic behavior may play in furthering coexistence or competitive exclusion (Gause, 1934) at the interspecific level.

MATERIALS AND METHODS

Crabs were obtained by diving at three sites: Salisbury Cove and Laboratory Cove on the northeast shore of Mt. Desert Island and at Sullivan Harbor on the north shore of Frenchman Bay. Shells occupied by crabs were sorted into four, arbitrary size categories and the number in each set and the types of shells occupied recorded. Shell aperture diameter, measured at right angles to the columellar axis, was used at the basis for defining each set: small (1.0–9.9 mm), small intermediate (10.0–14.9 mm), large intermediate (15.0–19.9 mm) and large (above 20 mm). Correlation coefficients for regression curves calculated for crab weight against aperture diameter were highly significant (0.743, $P < 0.001$ and 0.636, $P < 0.001$ for *P. acadianus* and *P. pubescens* data respectively) so that division of crabs into any series of sets on the curve resulted in relatively slight overlap values between adjacent sets. Although other dimensional correlations may be more significant (Hazlett, 1970b) the one adopted proved a valid and convenient method for estimating crab size without the necessity of evicting animals from their shells subsequent to initial determinations. The shell adequacy index of Vance (1973a, 1973b) would have provided a more rigorous standard. One hopes that this index will be generally adopted for hermit crab studies, particularly in cases where crabs occupy a wide range of domicile shell types.

In field studies fifteen, square foot, bottom samples were taken along roughly determined "swim" lines at each collecting site in order to estimate the supply of empty mollusc shells. More complete analysis was hampered by strong tidal currents and low water temperature (11° C).

Experimental animals were held in circulating sea water tanks at 11° C–13° C and fed regularly with shredded mussel and clam. For some experiments ten to twelve crabs were crowded into 15×21 sq. cm plastic containers from 60 to 108 hours prior to testing or individually isolated in the compartments of plastic, perforated ice-cube trays covered with sheets of perforated plexi-glass in running sea-water. All behavioral tests were conducted in 35×35 sq. cm polythene trays provided with running sea-water and a substratum of washed gravel.

For purposes of uniformity, most tests were run with crabs in the small intermediate set which contained animals with a shell aperture range between 10.0 and 14.9 mm and average crab weight/shell aperture indices of 3.16 ± 0.83 for *P. acadianus* and 2.68 ± 0.61 for *P. pubescens* collections. Crabs were generally selected from the 11–14 mm aperture range in order to avoid as many overlaps with other sets as possible. As preliminary tests showed none of the heightened

aggressiveness of small females reported by Reese (1962a) for other species of hermit crabs, animals were not sexed in the following investigations. No subject was used more than once in any of the trials reported below. Where necessary crabs were evicted from their domicile shells by applying an electric soldering gun at the shell apex.

Experiment I

In order to test the influence of shell abundance on shell selection, small intermediate sized crabs were evicted from domicile shells and allowed to enter *Littorina* shells whose aperture measurements were appropriate to crabs of the smallest size range. *Littorina* and *Thais* shells were arranged at equal intervals around a perimeter surrounding a centrally placed container from which crabs were released into the test chambers. The ratio of *Littorina* to *Thais* shells varied in the different tests, as follows: 5 : 2, 2 : 5, and 4 : 4. Each test was terminated at twelve hours and the type of shell occupied by the crab recorded. Previous experience indicated that crabs seldom exchanged shells after a twelve-hour period under similar conditions.

Experiment II

Tests were conducted to see if a difference existed between the two crab species in their preference for shells colonized by the hydroid *Hydractinia echinata*. In one group of trials crabs evicted from *Littorina* domicile shells were given the choice of entering either of two *Littorina* shells of the same size, one bare and one covered with a *Hydractinia* colony. In each of second series of trials a crab with a bare domicile shell was released in the presence of an empty, *Hydractinia*-colonized shell. All of the above trials terminated after twelve hours when the type of shell occupied was recorded.

Experiment III

Investigations were designed to compare conspecific aggression in the two crab species. In each trial a pair of crabs was released in the test area for a ten-minute period, this being sufficient time for crabs to establish dominant/subordinate relationships. Dominant crabs showed aggressive display by extending their chelipeds forward, by vertical rotation of their shells and by rising on their ambulatory legs. Dominance was considered to be established when one crab of a pair persistently retreated at the advance of the other or was repeatedly forced into submissive positions. Threat and intimidation often were followed by direct assault which resulted in the eviction of subordinate individuals from their shells in a manner similar to the behavior reported by Hazlett (1967, 1970a, 1972b) for a number of hermit crab species including *Pagurus pubescens*. In the present tests eviction positioning was recorded as additional evidence of dominance and trials were concluded before the end of the test period as soon as this position was assumed by the dominant crab.

In another series of tests crabs which had been either isolated or crowded from 60 to 108 hours were tested for dominance in trials each of which utilized one isolate and one recently crowded individual. In another group, dominance
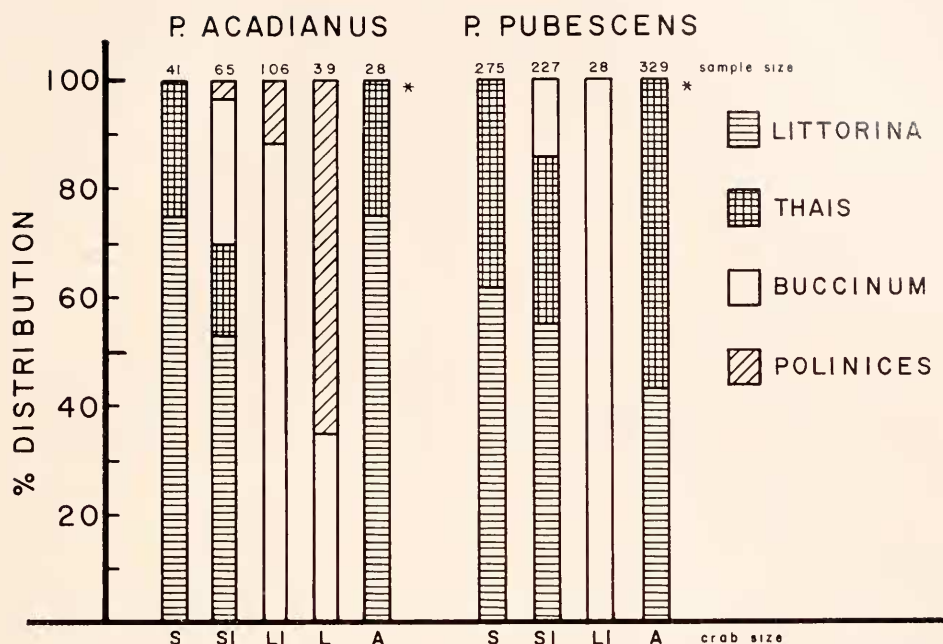
FIGURE 1. Per cent distribution of mollusc shell types occupied by different size categories of *Pagurus acadianus* and *P. pubescens* from pooled samples and collections from Sullivan Harbor(*). Crabs from the latter area were with few exceptions in the small and small-intermediate size range. Abbreviations for size categories are: S, small; SI, small intermediate; LI, large intermediate; L, large; A, all sizes.

tests were performed between animals occupying different shell sizes relative to their body weights. Dominance was recorded between crabs in normal size shells (appropriate crab weight/shell volume or aperture index) and individuals of the same size range housed in shells of inadequate dimensions *or* between animals occupying small and large shells (high and low crab weight/shell volume index respectively).

<div align="center">RESULTS</div>

Field data and observations

The distribution of shell types occupied by different size groups of *P. acadianus* and *P. pubescens* from pooled samples of all collecting sites and from the Sullivan Harbor collections is shown in Figure 1. Shells principally occupied by crabs were *Littorina littorea, Thais lapillus, Buccinum undatum* and *Polinices heros*. In both species individuals in the two smallest size groups were found principally in *Littorina* and *Thais* shells. The overlap value in terms of the proportion of shells occupied in common by crabs of each species was 84%. Larger crabs occupied shells of *Buccinum* and *Polinices* at a lower overlap value of 42%. These data support previous analyses by Lindsey and Grant (1970). It is important to note the relative numbers of shell types within each category of crab size, and to compare data from pooled samples with those from Sullivan Harbor. At this
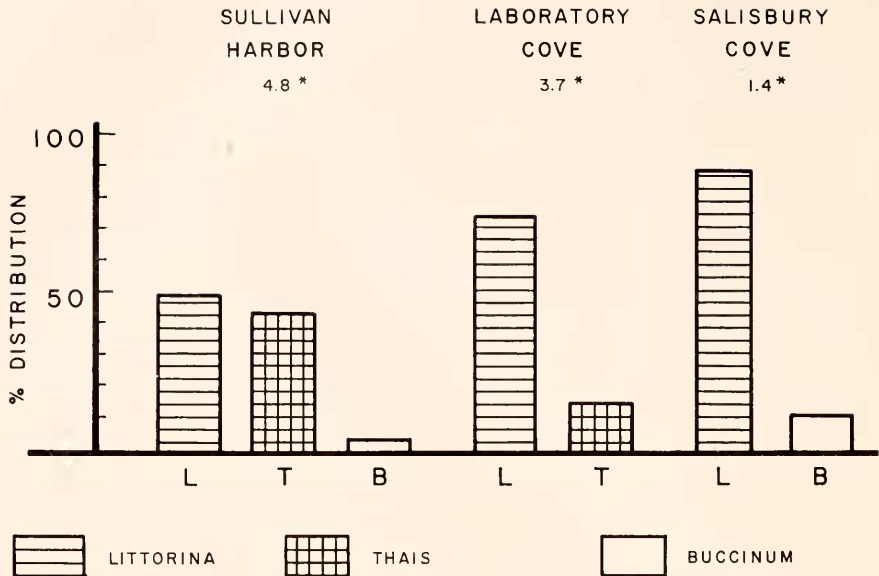
FIGURE 2. Average per cent distribution of empty mollusc shells collected in fifteen square foot samples from each of three localities in Frenchman Bay. Ninety-six per cent of all shells collected were in the smallest size range. Asterisk indicates mean number of empty shells per square foot.

location a higher proportion of the *P. pubescens* population occupied *Thais* shells than elsewhere, relatively few specimens of *P. acadianus* were collected and an overlap value of 63% was recorded. Twenty-seven per cent of the *P. acadianus* specimens were found in shells covered with colonies of the hydrozoan, *Hydractinia echinata*. Only one individual of *P. pubescens* was recorded in a *Hydractinia* covered shell out of 529 captures. It is interesting to note that hydrozoans were not found on any shells containing living molluscs within the area of study.

Field observations at a number of locations indicated that individual, larger sized *P. acadianus* are widely spaced. They tend to occupy elevated areas such as rocks which protrude from a surrounding area of low sand or low gravel. *P. pubescens* and small *P. acadianus* individuals on the other hand, most commonly were found closely spaced in areas around wharf pilings and on vertical faces of rock wall though *P. acadianus* individuals appeared more widely dispersed. In such assemblages crabs do not appear to maintain individual distances as such or to form closely spaced aggregates.

Most empty shells collected in the field survey were small size *Littorina* and *Thais* shells (Fig. 2). Their density was highest at Sullivan Harbor where the proportion of *Thais* to *Littorina* shells was greater than in Laboratory Cove. No *Thais* shells were collected in Salisbury Cove.

Behavior studies

Experiment I. The results of tests conducted to see if relative abundance of different types of shells influences crab selection are given in Table I. *P. acadianus*

TABLE I

Shell availability studies: results of twelve hour selections by individual crabs presented with empty mollusc shells in different species ratios. All animals were small intermediates; P values determined by χ^2

Pagurus acadianus		Shell selection	
Shell ratios Littorina/Thais	No. trials	Littorina	Thais
5/2	12	11	1
2/5	12	9	3 $P < 0.05$
4/4	13	11	2 $P < 0.02$
Pagurus pubescens			
5/2	10	7	3
2/5	12	2	10
4/4	15	9	8

test animals chose *Littorina* shells more often than could be predicted on the basis of shell-type ratios except in those trials where *Littorina* shells were the most abundant type, whereas *P. pubescens* individuals chose shell types in proportion to their relative abundance.

Experiment II. Table II gives the results of experiments which tested the preference of individual crabs evicted from their domicile shells when given the choice between a bare shell and one *Hydractinia* colonized shell. The number of trials in which crabs chose shells with *Hydractinia* colonies was significantly higher for *P. acadianus* and significantly lower for *P. pubescens* test animals than could be predicted on the basis of random selection.

In each of the second trial series, individuals of *P. acadianus* were recorded in colonized shells at the end of the twelve hour test period in all but two cases, while only one *P. pubescens* crab abandoned its domicile shell (Table III). Considering the preference shown by evicted crabs for previously occupied domicile shells (Grant, 1963), the large number of *P. acadianus* individuals which abandoned domiciles in the above trials supports the view that the species has a strong preference for shells colonized by *Hydractinia*. The species of shell colonized did not appear to affect the results.

Experiment III. As pilot tests demonstrated little agonistic behavior at the inter-specific level between individuals of *P. acadianus* and *P. pubescens,* the experi-

TABLE II

Selection by evicted crabs of shells with and without Hydractinia colonies.

	No. trials	Select colonized Littorina shell	Select bare Littorina shell	Sign test
P. acadianus	39	29	10	$P < 0.02$
P. pubescens	40	10	30	$P < 0.02$

TABLE III

Selection of shells with Hydractinia *colonies. Each trial represents a choice made by a crab in its home shell presented with a* Hydractinia *covered shell of appropriate size:*
L = Littorina; T = Thais; B = Buccinum.

No. trials	Home shell type	Colonized shell type	No. selecting home shell	No. selecting colonized shell
		P. acadianus		
15	B	B	2	13
10	L	L	0	10
3	L	P	0	3
		P. pubescens		
6	B	B	6	0
12	L	L	11	1
4	T	L	4	0
4	L	T	4	0

ments reported below were limited to comparisons of conspecific aggression in the two species.

Isolated individuals of *P. acadianus* showed a significantly higher incidence of dominance over crowded individuals in most trials and assumed eviction positions in nearly half of those trials in which they were dominant (Table IV). That the period of isolation may effect level of aggressiveness is suggested by the fact that the percentage of 108 hour isolates achieving dominance and taking eviction positions was slightly higher than for those isolated 60 hours, although the differences were not significant. No agonistic behavior was recorded in any of the trials

TABLE IV

Results of conspecific dominance tests between isolated and crowded individuals

	No. trials	No. isolates dominant	No. crowded dominant	P (sign test)	No. isolates assuming eviction position
		Pagurus acadianus			
Pooled data	44	32 (72.72%)	11 (25.00%)	P < 0.01	13 (43.75%)
60 hr	25	17 (68.00%)	8 (32.00%)	P < 0.05	5 (28.82%)
108 hr	19	15 (78.04%)	3 (15.78%)	P < 0.01	8 (53.33%)
		Pagurus pubescens			
60 hr and 108 hr	34	No agonistic behavior recorded between isolated and crowded individuals			

Dominance not established in one trial.

with *P. pubescens* crabs, suggesting that the level of aggression, in the species is influenced neither by isolation nor aggregation.

The results of another series of dominance tests in which test animals occupied different shell sizes relative to body weight are shown in Figure 3. Most individuals of both crab species which occupied inadequately small shells (high crab weight/shell volume index) were dominant over animals housed in domicile shells of adequate size. Dominance was evenly distributed in tests between individuals of *P. acadianus* occupying normal and overly large shells. No agonistic behavior at all was recorded for individuals of *P. pubescens* in similar trials. In other tests of this series in which dominance was recorded between paired crabs occupying small and large shells, *P. acadianus* crabs displayed agonistic behavior in every trial and dominance ranking between small and large shelled individuals was approxi-
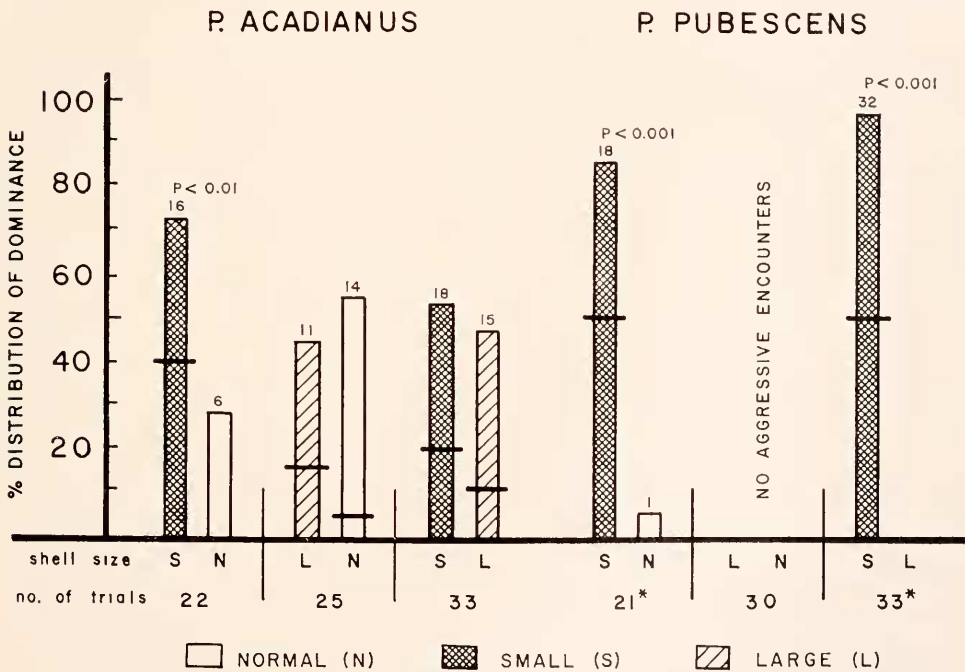

FIGURE 3. Results of con-specific dominance tests in *Pagurus acadianus* and *Pagurus pubescens* between paired individuals in different size shells according to crab weight/shell volume indices. The proportion of trials in which dominant crabs assumed eviction positions is shown by the area below the heavy horizontal lines on the graphs. In some trials no aggressive behavior was recorded.

mately even. However, small-shelled crabs of *P. pubescens* were dominant in most trials and half of the dominant individuals assumed eviction positions.

DISCUSSION

It is important to consider the above results in terms of the relative impact which hermit crab behavior may have on influencing ecological overlap between

the two species under study. Such discussion assumes that mollusc shells constitute an essential resource to the crabs which is roughly analogous to territories, nesting sites, *etc.* of other animals.

On the basis of crab weight/shell aperture indices, *etc.*, it is clear that a large proportion of the *P. acadianus* population exceeds the size range of *P. pubescens* individuals in the study areas. The larger specimens of *P. acadianus* principally inhabit *Buccinum* and *Polinices* shells and thus are not in competition with smaller individuals of *P. pubescens* for suitable domiciles. In the smaller size categories *Littorina* and *Thais* are by far the most common genera of shells occupied by both crab species down to the very smallest individuals. Laboratory studies suggest that *P. acadianus* has a distinct preference for *Littorina* shells even if they are in relatively low supply. *P. pubescens*, however, selects shells in rough proportion to their relative abundance suggesting that shells constitute a "fine-grained" resource (Levins, 1968) for this species. Thus where *Littorina* provides a single resource for domicile shells the two crab species may be in direct competition. Where both *Littorina* and *Thais* shells are available both species may coexist but where *Thais* shells predominate *P. pubescens* could have a competitive advantage. Although field surveys were not extensive enough to be conclusive they tend to support this general assumption. In Sullivan Harbor where the density of *Thais* shells was highest the number of *P. pubescens* was proportionately greater and a larger percentage of the population occupied *Thais* shells than elsewhere. This suggests that resource partitioning may be a more important mechanism furthering coexistence of hermit crab species in Frenchman Bay than in the case of the sympatric species of intertidal crabs studied by Vance (1973a). The preference of *P. acadianus* individuals for *Hydractinia* colonized shells could serve to separate resources and thus favor coexistence with *P. pubescens* even in areas as Salisbury Cove where *Littorina* provides the sole resource of domicile shells.

The failure to find empty shells in large size ranges raises another problem which may be closely related to behavior and individual fitness (Childress, 1972) in *P. acadianus*. *Buccinum* shells which constitute the major domicile resource of larger crabs are relatively fragile and subject to breakage by wave action. Thus empty shells are limited in supply and those shells already occupied by crabs will constitute the bulk of the available resource. As *Hydractinia* grows slowly and does not occur on shells containing living molluscs in the study area, *Buccinum* and *Polinices* shells colonized by the hydrozoan may constitute natural "heirlooms" which are occupied by successive generations of crabs over a period of years.

Schijfsma (1935) was unable to demonstrate a predeliction for *Hydractinia* covered shells in *P. bernhardus,* a species closely related to *P. acadianus.* However, recent investigations by Jensen (1970) and Wright (1973) working with *P. bernhardus* and with *P. longicarpus* and *P. pollicaris* respectively, confirm our observations that some hermit crabs do show strong, preferential selection for *Hydractinia.* Wright's suggestion that *Clibanarius vittatus* is seldom found in *Hydractinia*-covered shells because crabs are exposed during low tides at temperatures exceeding the tolerance range of the hydroids is not applicable in the case of *P. acadianus* in Frenchman Bay where hermit crabs are never found above the sub-littoral zone even at high tide.

Aggressive behavior is pronounced in *P. acadianus*. This indicates that there may be considerable intra-specific competition for shells particularly among larger

crabs, a factor which could act to limit or regulate population growth. The fact that individuals of *P. acadianus* appear to be widely spaced in nature together with the increased ability of isolates to dominate encounters, suggests that maintenance of distance between individuals may be a behavioral strategy adapted to limited shell supplies in larger animals. As Grant (1963) and Berman, Francis and Grant (1973) have shown that this species is moderately errant, individual space rather than territoriality *per se* is probably one significant feature of their population dispersal. It might also be advantageous for aggressiveness to diminish under crowded conditions when crabs congregate on occasion at some common food source, a suggestion which is supported by the above investigations. Hazlett (1968c) has proposed that the increase in density of crabs within an area may come about slowly thus allowing time for adjustment and a decrease in levels of aggression. Specimens of *P. bernhardus* from the Clyde tend to clump together as density increases according to Kenneth Mitchell, University of Glasgow (personal communication). *P. pubescens* on the other hand appears to be a more closely spaced species and exhibits little agonistic behavior following isolation or when crowded. There is, however, no evidence that this species forms social groupings similar to those reported by Rossi (1971) for *Diogenes pugilator*.

According to Vance (1973b) aggressive levels were unaffected by shell size in *Pagurus hirsutiusculus* although the probability of larger crabs evicting smaller individuals during encounters increased as the size of their shells decreased. In *P. pubescens*, however, occupancy of inadequately small shells produces a marked increase in aggressiveness over the low levels usually displayed. Heightening of agonistic behavior also occurs in *P. acadianus* under similar conditions although it is less pronounced in this normally more aggressive species. Increased aggressiveness in hermit crabs which occupy shells too small by volume is understandable as a behavioral strategy to accommodate individual growth and is consistent with Hazlett's (1970b) view that shell volume provides a stimulus to aggression in crabs which have outgrown their domicile shells. Childress (1972) has shown that *Clibanarius albidigitus* individuals tend to "trade up" to shells larger than necessary and that this behavior enhances reproductive fitness based upon increase in clutch size. This, of course, would be most difficult where appropriate shells are limited in supply or are already occupied. Indeed Vance (1973a) has described situations in which larger hermit crabs were found occupying shells significantly smaller than preferred size.

The fact that neither *P. acadianus* nor *P. pubescens* individuals showed an increase in agonistic behavior when housed in large shells is interesting as Hazlett (1970b) found that increase in shell weight stimulated aggression in *P. bernhardus*. As species differences in threshold levels are to be expected it seems likely in the present studies that occupied shells, although large by volume, were not heavy enough to provide sufficient stimulus to increased aggression. In females it may be of selective advantage to avoid unnecessary combats if occupation of shells somewhat larger than necessary does promote an increase in reproductive potential as suggested by Childress (1972).

It seems reasonable to conclude on the basis of the present investigation that differential behavior in shell selection is sufficient to allow co-existence of *P. acadianus* and *P. pubescens* populations under most conditions. Where competition exists, however, it is probably not sustained by inter-specific shell fighting

per se as described by Hazlett (1970c) in hermit crab species from Hawaii. Agonistic behavior in both species studied is primarily a factor of conspecific competition.

Summary

Two species of hermit crab, *Pagurus acadianus* and *P. pubescens* are distributed sympatrically in offshore waters of Frenchman Bay, Maine. Laboratory and field investigations indicate that smaller sized specimens of *P. acadianus* have a preference for *Littorina* shells over *Thais* shells whereas *P. pubescens* individuals enter shells of either *Thais* or *Littorina* depending on the relative abundance of each type. Larger *P. acadianus* individuals which usually exceed the size range of *P. pubescens* principally occupy shells of *Buccinum* and *Polinices*. *P. acadianus* shows a strong preference for mollusc shells colonized by *Hydractinia echinata*.

Isolation increases the level of aggression in *P. acadianus* individuals, but the low levels of agonistic behavior found in tests with *P. pubescens* crabs appear not to be affected by changes in crab density. In both species, subjects in shells of too small a size by volume showed a high degree of dominance in trials over crabs occupying normal or large shells; a factor which can be considered an adaptation to accommodate individual growth.

It is concluded that behavior related to shell selection in the two species of crabs is sufficiently different to allow co-existence of the two species on the basis of resource partitioning, except in situations where smaller sized *Littorina* shells without *Hydractinia* colonies constitute a single resource base. However, there may be considerable intra-specific competition between larger specimens of *P. acadianus* for limited supplies of *Buccinum* shells and between crabs of all sizes located in appropriate sized shells and those which have outgrown their domicile shells.

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